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Ecological and evolutionary role of photobiont-mediated guilds in lichens

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Abstract

Lichens have arisen independently on several occasions and there have also been multiple losses of the lichen symbiosis in different fungal lineages. This pluralistic evolutionary history explains major patterns in the current diversity of lichens and the mixed occurrences of lichenized and non-lichenized species in many fungal groups. However, we still have an insufficient understanding of factors that induce re- and de-lichenization events and promote phylogenetic change in lichen symbionts over evolutionary time. While lichens are often cited as one classic example of coevolution, reciprocal evolutionary change between symbionts has been difficult to demonstrate. The apparent lack of phylogenetic tracking in many lichen groups indicates that a broader context is needed in which to interpret coevolution. This article provides some elements for such a framework and argues that the present diversity of lichen symbionts has evolved within an ecological kaleidoscope of photobiont-mediated guilds.

Keywords: Symbiosis, lichens, community ecology, evolution, coevolution, lichen guilds, fungi

Introduction

Lichen-forming species represent a major ecological group among the Fungi and especially among the Ascomycota with some 13 500 lichenized species. A majority of these fungi associate with symbiotic green algae, with only about 12% of all species having cyanobacteria as primary or accessory photobionts. Attempts to determine the photobiont at a species or strain level have only been made for a small fraction of all lichen species (Rikkinen, 2002).

Many important gaps in our current understanding of lichens are linked to problems in defining symbiotic systems within the rigid conceptual framework of fungal and algal taxonomy. Some lichens rely exclusively on vegetative reproduction, leading to innumerable genetically identical symbiotic units. Others start their development with the fusion of several symbiotic propagules, potentially representing different genets. In some lichens even a mechanistic

delimitation of a single thallus can be very difficult. Hence, should the intuitive difference between a single leprose lichen thallus and a group of foliose thalli be seen as a mere artifact of human perception of scale or is there basis for distinguishing between two different levels of organization? Are the later lichens being treated as 'individuals' purely for mechanistic convenience or does their biology actually center around this level of organization? Questions like these are important because different ecological factors are known to operate on different scales. Thus, the scales used may largely determine the range of patterns and processes that can be detected in ecological studies (Rikkinen 1995).

Molecular and phylogenetic methods have provided powerful new tools for investigating the diversity and ecology of lichens and many interesting patterns have already emerged. One is that lichen symbioses have independently arisen on several occasions and that there have also been many independent losses of the symbiosis in different fungal lineages (Gargas et al., 1995; Tehler et al. 2000; Lutzoni et al., 2001). Another important finding is that lichen-forming fungi are highly selective with respect to their photobionts (Rambold et al., 1998; Beck, 2002; Paulsrud, 2001; Rikkinen 2002). In most cases only a few closely related photobiont strains serve as the appropriate symbiotic partner for individual fungal taxa (Miao et al., 1997; Paulsrud and Lindblad, 1998; Paulsrud et al., 1998, 2000, 2001; Kroken and Taylor, 2000; Helms et al., 2001). On the other hand, many different species of lichen-forming fungi, sometimes from distantly related lineages, may house identical photobiont strains (Beck et al., 1998, 2002; Beck, 1999; Dahlkild et al., 2001; Piercey-Normore and DePriest, 2001; Oksanen et al., 2002; Rikkinen et al., 2002; Romeike et al., 2002; Summerfield et al., 2002; Yahr et al., 2002; Wirtz et al., 2002).

Communities, species assemblages and functional guilds

Lichens with similar environmental requirements tend to form characteristic species assemblages in specific habitat types. These sets of taxa are usually called lichen 'communities' (Barkman, 1958; Wirth, 1972; James et al., 1977; Nimis, 1991). The fundamental criticism against these units questions whether they really represent distinct ecological entities. 'Species assemblage' may be the most appropriate term for the groupings of species whose patterns of organization, except co-occurrence, are largely unknown (Rikkinen 1995). Against this background is quite interesting that many mycobionts are so selective with respect to their photobionts and often share similar symbionts with some, but not necessarily all, neighboring lichens (Paulsrud et al., 1998, 2000, 2001; Rikkinen et al., 2002; Romeike et al., 2002; Wirtz et al., 2002). This indicates that many lichen communities involve one or several photobiont-mediated guilds. These are co-occurring species populations of fungi that utilize specific photobiont strains in similar ways and

potentially interact with horizontal linkages (Fig. 1). The guilds can be further divided into taxon guilds which represent species populations within one taxonomic or functional subclass of a photobiont-mediated guild (Jaksic, 1981; Giller and Gee, 1987; Rikkinen, 1995).

For example, many epiphytic macrolichens with cyanobacterial photobionts depend on a restricted group of closely related *Nostoc* strains. The mycobionts of these lichens share a common pool of photobionts and thus form an ecological assemblage, the *Nephroma* guild. Conversely, many predominately terricolous cyanolichens depend on a different group of closely related *Nostoc* strains, thus forming the *Peltigera* guild (Paulsrud et al., 1998, 2000, Lohtander et al., 2002; Rikkinen et al., 2002). Both guilds are well represented in mature and old-growth forests in humid boreal and temperate regions. The difference in the overall substrate preferences of the two guilds is by no means abrupt nor oblicatory. Terricolous and epiphytic lichen habitats form an ecological continuum, which itself is strongly influenced by microclimate, nutrient status and other site factors. Thus, in suitable habitats, like on the basal trunks of old deciduous trees and on moist rock-faces, members of both guilds co-occur and frequently form species-rich communities. Similar photobiont-mediated guilds are certainly common among the green algal lichens (Rikkinen, 1995; Beck et al., 1998; Beck, 1999, 2002; Kroken and Taylor, 2000; Piercey-Normore and DePriest, 2001; Tibell, 2001; Tibell and Beck, 2002).

Fungi within a guild may interact on different levels of community organization. For example, some lichen-forming fungi may largely depend on other guild members for the effective dispersal of their photobionts. Many structures and different mechanisms are involved in the reproduction and dispersal of lichens (Meier et al. 2002). The symbionts may produce their own diaspores, but many lichens also facilitate the reproduction and simultaneous dispersal of the whole symbiotic consortium. This is achieved via thallus fragmentation or by producing more specialized symbiotic propagules, such as soredia and/or isidia. The mycobionts of some lichens are rarely or never fertile and obviously depend on symbiotic propagules. However, in most cases the lichen symbiosis seems to be re-established at each reproductive cycle (Rikkinen, 2002).

Both principal modes of dispersal are often represented among the different lichen species of a photobiont-mediated guild (Fig. 1). Under such circumstances, it is unnecessary for all the mycobionts to produce symbiotic propagules, as other guild members will very effectively disperse the same photobiont. Thus, the dispersal ecologies of many guilds may involve core species that produce huge numbers of symbiotic diaspores. Fringe species can use their resources to produce innumerable fungal spores, but by doing so, they tend to become partly dependent on the core species for their photobionts (Rikkinen, 1995; Rikkinen et al. 2002). Some fringe species are

aggressive enough to steal photobionts from other guild members (Friedl, 1987; Beck et al. 2002). Such thefts may be common, as the germinating spores of many fringe species are more likely to encounter lichenized than free-living photobiont cells. Aposymbiotic lichen photobionts are not conspicuous in most natural habitats and many fringe species probably obtain their photobionts from pre-existing juvenile stages and/or senescent thalli of other guild members (Rikkinen, 1995). Innumerable symbiotic propagules inevitably land on suboptimal substrates, eventually disintegrate and potentially release some living photobionts. These can be salvaged by fringe species, many of which probably have slightly different substrate preferences than the core species (Sanders and Lücking, 2002). If a lichen mycobiont is initially unable to establish an association with an appropriate photobiont, it can sometimes temporarily exploit other types of algae or cyanobacteria (Ott, 1987; Gassmann and Ott, 2000). Furthermore, some lichen mycobionts may survive aposymbiotically for extended periods (Etges and Ott, 2001).

Core species benefit from the activity of fringe species, as photobionts from their misfortunate diaspores are salvaged into other guild members, rather than being completely lost. Without the ability to produce symbiotic propagules, the fringe species will not transport the photobionts into new sites, but they can promote the success of their guild on a local scale. While many lichen photobionts are poorly equipped for independent existence, they probably reproduce just as effectively within fringe species as in core species. Eventually, when the fringe species dies and disintegrates, some of its photobionts are released for the potential benefit of all other guild members in the same habitat (Fig. 1).

In lichens the mycobiont mediates most interactions between the photobionts and the outside world and, by doing so, it cushions the impacts of many environmental extremes. As different lichens have different defences, environmental changes will rarely affect all lichens within a local community with equal intensity. Thus, a wide spectrum of compatible mycobionts can effectively increase photobiont resistance against grazing, pathogenic fungi and other detrimental factors. As long as even a few photobiont cells survive, they can significantly promote the re-colonization of the whole fungal guild. It is easy to imagine how the photobionts benefit from this situation: a large number of unrelated, compatible mycobionts widens their microhabitat range and increases the likelihood of survival both within single habitats and during the critical dispersal phase. One might thus expect an evolutionary trend towards sharing of photobionts by many unrelated fungi within specific environments and geographical regions. This trend could be most pronounced in harsh environments, like in the Antarctic, where many lichen-forming fungi seem to exhibit relatively low degrees of photobiont specificity (Romeike et al., 2002; Wirtz et al., 2002).

It is not necessary for all fungal species within a photobiont-mediated guild to live in the same habitat or even belong to the same community. Some characteristic species assemblages with many fertile species, but without obvious core species could develop as 'side-products' of dispersal activity within neighboring communities. The dispersal ecologies of such assemblages could mainly reflect the density dependent nature of lichen dispersal, i.e., when the input of symbiotic diaspores is large enough, many photobionts are released into microhabitats that are totally unsuitable for the core species itself. These photobionts can be freely salvaged by fungi that are better-equipped to live in those particular habitats. This underlines the problems of ecological lichen studies that concentrate on single habitat classes, like on the twigs or trunks of specific tree species within a limited study area. Colonization between habitat classes may have a dramatic effect on community structure and any attempts to delimit lichen guilds should include an evaluation of interhabitat effects, often over a wide range of different spatial scales (Rikkinen, 1997).

James et al. (1977) emphasized that lichen sociology should aim to determine those major noda in the continuum of lichen species assemblages, which are related to recognizable ecological and environmental parameters. Many lichen communities that have been recognized by intuitive methods or by analyzing data obtained with randomized sampling techniques are likely to include species from several photobiont-mediated guilds. Further studies of guild structure may help to identify functional units within these communities and give a more solid basis for studying the assemblages as symbiotic processes. Eventually this can lead to a better understanding of community organization in lichens and reveal many ecological parameters that have remained hidden in former studies.

Evolutionary role of lichen guilds

The present diversity of lichen-forming organisms has evolved within a constantly changing matrix of ecological guilds. The guilds are hardly a new phenomenon – some of them are ancient, probably much older than some of the symbiont species presently involved (Fig. 2; Taylor et al., 1997; Printzen and Lumbsch, 2000; Peterson, 2000; Poinar et al., 2000; Rikkinen and Poinar, 2000, 2002; Printzen and Ekman, 2002; Rikkinen, 2002). The ecological boundaries between existing guilds may appear steep, but on an evolutionary timescale they have been crossed rampantly. This is strongly supported by the fact that many guilds include fungi from several different genera or even

families. Concurrently, closely related fungi may often associate with different types of photobionts and thus belong to different guilds.

For lichen-forming fungi, each successful shift into a new guild provides new opportunities for specialization and subsequent radiation. Each newcomer also has the potential to shift the pre-existing balance between other members of the guild. This can cause new selection pressures also against fungi that themselves did not shift guilds. Some species-rich clades of lichen-forming fungi may have arisen from endemic species after some ancestral populations managed to shift into a new guild with closely related photobiont strains, preferably with rather indistinct strain boundaries but with subtle differences in environmental requirements. On the other hand, some endemic lichens may have evolved from more widely distributed species after some fungal populations sifted into geographically restricted guilds. In between these two extremes are many other possible scenarios. One consequence of guild shifts is that the photobionts that are the mainstay of certain fungi today are not necessarily the same as those that were utilized by the ancestors of the mycobionts only a few million years ago. Concurrently, even if some symbiotic algae are now only associated with certain fungi, these may not necessarily have been the initial selection agent on those photobionts (Thompson, 1994).

While the evolution of lichen guilds may often have begun as a pair-wise interaction or as an association between a few participants, additional symbionts have been collected over time, and others lost. Molecular recognition mechanisms of lichens may favor the evolution of polymorhisms, in which different symbiont populations differ in their companions. Furthermore, as already described, a relatively high level of symbiont promiscuity may be, not only beneficial, but required for the evolutionary success of lichen photobionts. Many photobionts have probably evolved to specialize on – and coevolve with – more than one fungal species simultaneously. Together all these effects may explain why the existence of competition is often difficult to demonstrate in lichen communities.

Some lichenicolous fungi have evolved from lichenized ancestors – they continue to depend upon specific photobionts without the need to find an appropriate free-living symbiont during each reproductive cycle (Rambold and Triebel, 1992; Peršoh and Rambold, 2002; Lawrey and Diederich 2003). Concurrently, the host ranges of these fungi may often appreciate guild boundaries. There may also have been some cases in which non-lichenized organisms have managed to enter into established lichen guilds. For example, the evolution of some basidiolichens may include examples of this (Sanders and Lücking, 2002). While gains of lichenization have probably been relatively infrequent, there may have been multiple losses of the lichen symbiosis in different fungal lineages.

As a consequence, several lineages of exclusively non-lichenized fungi have derived from lichen-forming ancestors (Lutzoni et al., 2001).

Many lichen genera include pairs or groups of closely related taxa that differ in their prevailing mode of reproduction. The taxonomic status of these morphs has evoked considerable interest among lichenologists (Poelt, 1970, 1972; Robinson, 1975; Tehler, 1982; Culberson, 1986; Mattsson and Lumbsch, 1989; Kärnefelt, 1997; Myllys et al., 1999; Kroken and Taylor 2001). In classical species pairs, the sorediate morphs have been called secondary species and the fertile morphs primary species, based on the assumption that the sorediate forms have evolved from fertile ancestors and never *vice versa*. In any case, specialization in symbiotic dispersal is not an evolutionary dead-end. For example, Ekman and Tønsberg (2002) found that most species of *Lepraria* and *Leproloma* form a distinct monophyletic group tracing back to a single common ancestor that switched from a sexual to an asexual mode of dispersal. The subsequent evolution and considerable speciation within this group has taken place in the absence of sexual processes. In this context elucidating the possible roles of guild level interactions offers exciting possibilities for future research. Both sexual and asexual species can clearly play important roles in lichen evolution, but these roles are typically manifested on different scales. While typical core species themselves may rarely give rise to new clades, they can drive the evolution of many other species within their guilds. One could speculate that evolutionary feed-back from other guild members is one mechanism that helps to maintain species coherence in sterile core species. On the other hand, guild shifts could explain the rise of some new species in asexual lichen groups.

As a whole, there are many interesting relationships between the molecular mechanisms of symbiont specificity, different paces of evolution in different symbionts, co-specialization of many fungi to a more limited number of photobiont strains, spatial structure of lichen guilds, and the diversification of lichen symbionts over evolutionary time. Reciprocal evolutionary change between pairs of symbionts is probably only the raw material for a broader pattern of coevolution that shapes relationships within functional lichen guilds. The tendency for some lichen symbionts to switch guilds over evolutionary time will almost invariably create networks of highly coevolved and less coevolved participants. For this reason alone, standard comparative phylogenetic methods will usually only reveal narrow glimpses of coevolution between lichen symbionts. By ignoring the guild scale, we may seriously underestimate the extent of coevolution between lichen-forming organisms.

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FIGURES

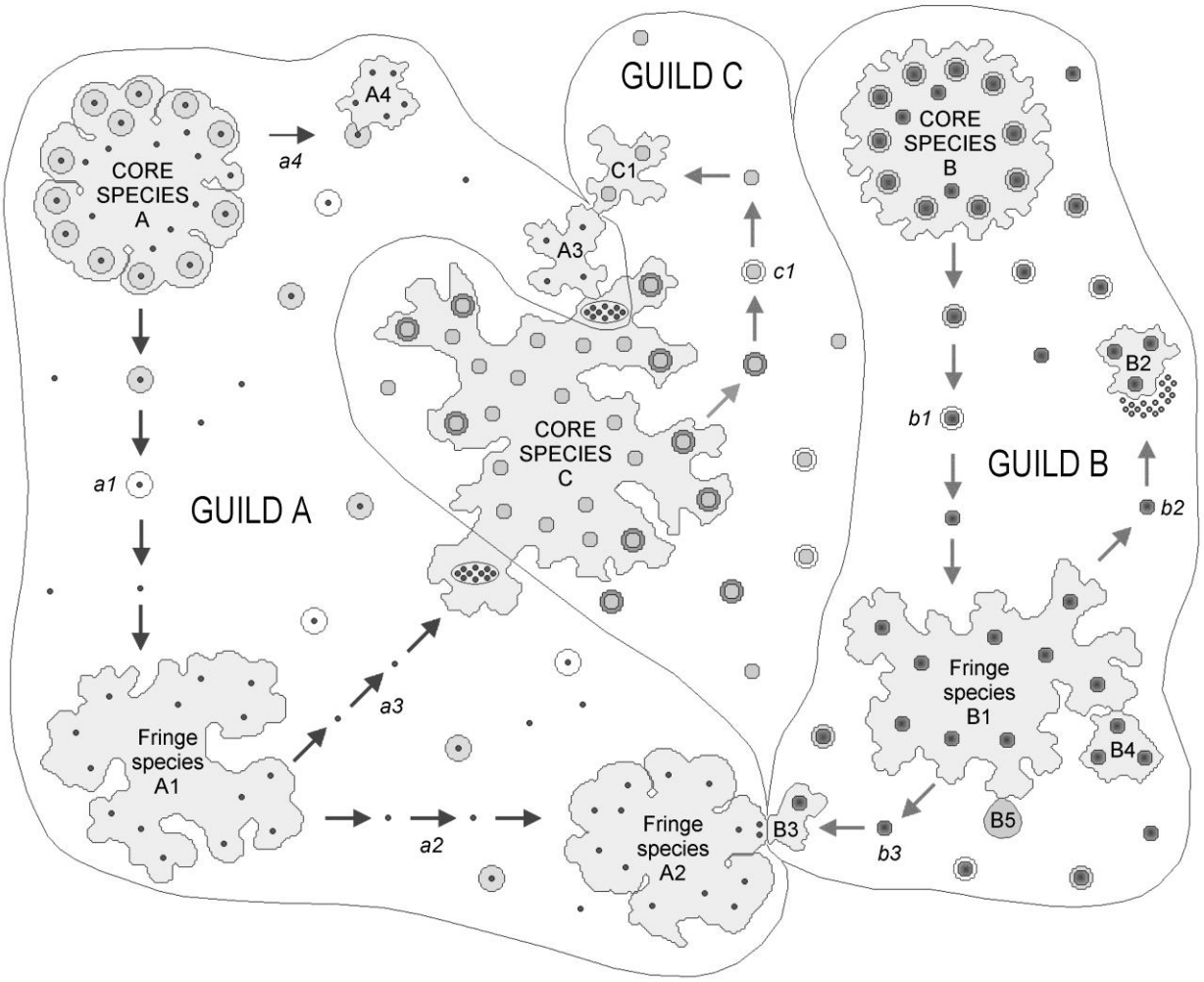

Figure 1. Schematic example of guild structure in lichens. The lichen-forming fungi belong to three different guilds (A, B, C), one centring around *Nostoc* cyanobacteria (A), one around *Trebouxia* green algae (B), and another around *Coccomyxa* green algae (C). As the lichen in the middle houses both *Coccomyxa* and *Nostoc* (in cephalodia), its mycobiont actually belongs to two guilds (C and A). As the symbiotic diaspores of the lichen only contain the mycobiont and green algal photobiont, the fungus is a core species in guild C and a fringe species in guild A. Under certain conditions this fungus can give rise to cyanobacterial morphotypes (A3) and/or green algal thallus lobes (C1). All core species produce masses of soredia, most of which will not develop into mature thalli (*a1*, *b1*). Numerous fringe species exploit the photobionts released from disintegrating soredia. At the latest when a thallus of a fringe species dies, some photobionts are released for the common benefit of the whole guild (*a2–a3*, *b2–b3*). Without the ability to produce symbiotic diaspores, a typical fringe species cannot export photobionts from the local substrate. Some fringe species are aggressive enough to take photobionts from juvenile stages of other species (A4),or live as lichenicolous lichens (B4) on other members of the same guild. The juvenile stages of many green algal lichens can establish loose cyanotrophic associations with free-living cyanobacteria (B2) and/or cyanolichens (B3). Some lichenicolous fungi (B5) have evolved from lichenized ancestors and also their host ranges appreciate guild boundaries.

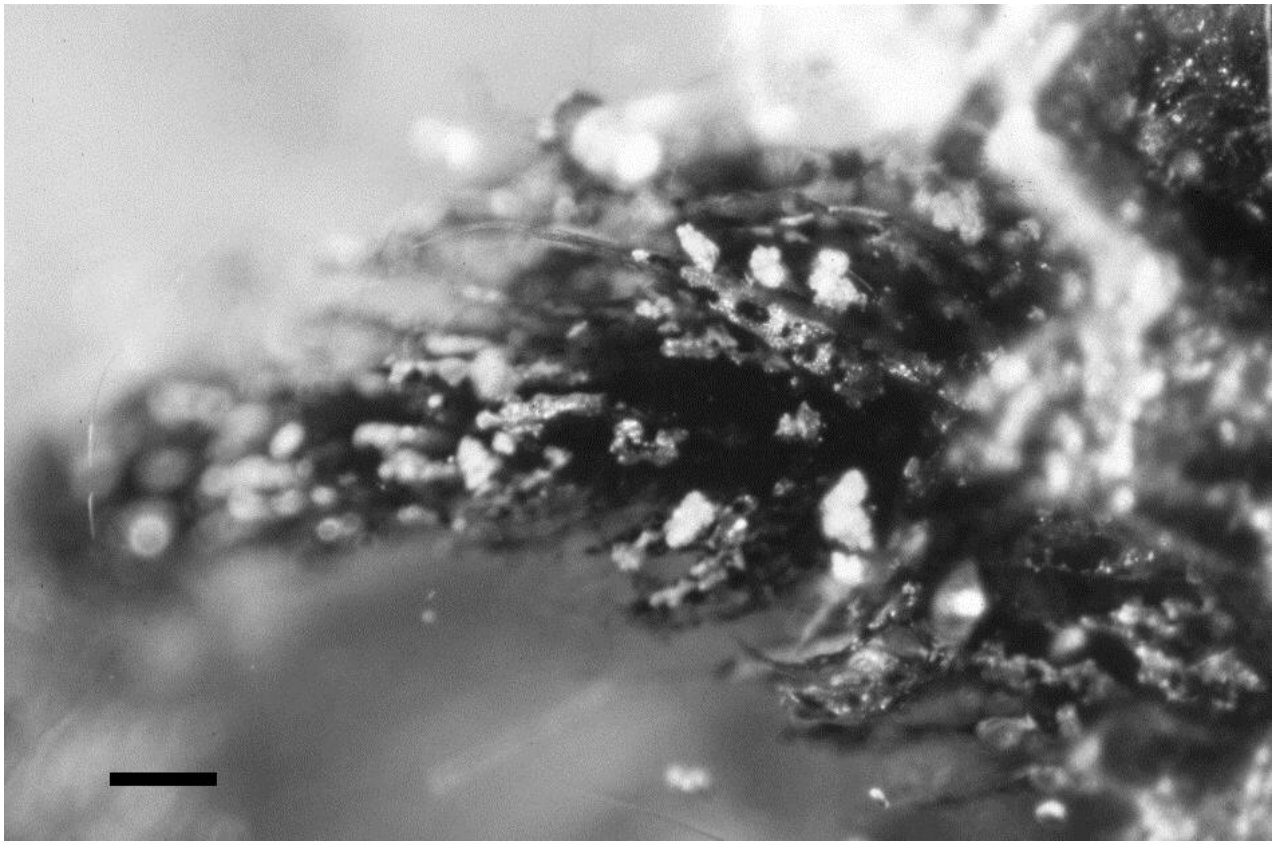

Fig. 2. Fossilized pre-thallus stages of lichen in Baltic amber. The amber specimen (Oschin 5/01) is 35–55 million years old. Scale bar = 1.0 mm.